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THE MORPHOLOGY OF THE HEAD OF *AESHNA CYANEA* (MÜLLER) (ODONATA: ANISOPTERA).

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With 7 Text-figures.

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1. Introduction.

The Odonata is usually held to be an ancient and specialised order and not ancestral to any of the other insect orders. It is therefore of interest to compare the structure of the Odonata with that of insects such as Orthopteroids, which are thought to show the basic structure of Pterygote insects with reasonable completeness.

The thorax of adult Odonata has been studied in detail (Clark, 1940; Sargent, 1937). The following is the first detailed and complete account of the morphology of the Odonatan head. Various aspects of head morphology have been discussed in the past. Strenger (1952) has given a description of the skeleton of the adult cranium, mandibles and maxillae and most of the associated muscles. She has, however, overlooked much previous work.

I wish to thank Lt.-Col. F. C. Fraser for advice on literature.

2. Nomenclature and Material.

The nomenclature is that of Fraser (1949). Adults and final instar nymphs of *Aeshna cyanea* (Müller) were examined by dissection of alcohol-fixed material. Polarised light was also used in the study of muscles.

3. Terminology.

The terminology used is that of Snodgrass (1928, 1935, 1947, 1950, 1951, 1952). Muscles have been given numbers corresponding with those given to their homologues in Orthoptera by Snodgrass (1928).

4. The Morphology of the Head.

Only the most important features are discussed since the diagrams will suffice for all routine description. The head of the nymph and that of the adult are discussed together.

(a) *The cranium.*

One of the most conspicuous features of the cranium is the development of the compound eyes (figs. 1A, 4E, *e*). The antennae (*ant*) are, in contrast, relatively small.

In the nymph where the compound eyes are not developed to the same degree as those of the adult, the sulci and accompanying ridges of the cranium show no marked specialisations. The epistomal ridge (fig. 1D, *er*), for example, is well developed but not conspicuous.

In the adult there are marked ocular ridges (fig. 5B, *or* (*l*)). Transverse epistomal (fig. 4A, *es*) and frontal (*sfra*) sulci connect the ocular sulci (*os*) on the anterior surface of the head and brace the cranium against distortion. The frontal muscles (fig. 6A, B, 2, 3, 38 and 35, 36, 39) have origin on the apodeme (*fra*) associated with the frontal sulcus. The frons (fig. 4A, *fr*) and the postclypeus (*pclp*), which are the cranial areas lying between the ocular, epistomal and frontal sulci, are arched. An arched area of skeleton lying between sulci is a familiar strengthening device, the ridges of the sulci acting as the "abutments" of the arch (see Short, 1951). On the posterior surface of the cranium there is a well developed occipital sulcus (fig. 4B, *ocs*) and ridge.

Sokal (1947) has given a lengthy description of the head capsule of *Pantala*. The figures, although detailed, are not clear. A general description of the Odonatan head is given by Lew (1934). Mittelstaedt (1950) has given a very general description of the cranium and tentorium of *Anax*. Grieve (1937) has given a good verbal description of the muscles of the nymphal stomodeum. The lateral dilators of the pharynx arising on the parietals described by Grieve were not seen in *Aeshna*.

(b) *The tentorium.*

The tentorium of the nymph (fig. 1D) and that of the adult (fig. 5C) are basically similar in form. In both cases the anterior arms (*at*) have origin in the pleurostomal part of the subgenal sulcus and are continuous with the pleurostomal ridges (fig. 5B, *pr*). In the nymph the dorsal arms of the tentorium (fig. 1D, *dt*) are attached to the cranium by small non-muscular fibres. In the adult each dorsal arm (fig. 5B, *dt*) is firmly fused with the ocular ridge of its side. These points have been noted by Snodgrass (1951). Lew (1934) states that the external tentorial pits of the adult are completely closed. This is not so in *Aeshna*. Hudson (1948) has given a description of the tentorium,

concentrating on details of the skeleton and ignoring the musculature. This type of study is of limited value.

In the origin of the anterior arms from the pleurostomal sulcus and its in π-shaped form the tentorium is probably primitive (see Snodgrass, 1935). It differs in form from the X-shaped tentorium of Orthopteroids.

(c) *The hypopharynx.*

In the nymph the dorsal hypopharyngeal muscles (fig. 2A, 38) and the adductors of the mandible (*admdh*) have insertion on a pair of sclerotic bands extending from the anterior end of the hypopharynx to the anterior and ventral surface of the stomodaeum. These sclerotic bands (*sh*), which are joined by an anterior median band, may be homologised with the suspensorium of the hypopharynx of Orthopteroids. On the posterior end of the hypopharynx is a pair of sclerotic bands (fig. 2C, *bsh* (*as*)) which fuse posteriorly to form a long sclerite attached to the postlabium. Snodgrass (1951) calls the posterior part of the sclerotic bands the anchor sclerite. However, the sclerotic bands may be homologised with the basal sclerites of the hypopharynx of Orthopteroids. The retractors of the hypopharynx (fig. 2A, C, 32) insert on these sclerites and have origin on the tentorial bar (*tb*) as in Orthopteroids. The prelabial flexors (*f*), having origin on the basal sclerites, have no obvious homologue in Orthopteroids and will be discussed below in the section on the labium.

In the adult (fig. 5D) the major difference is in the reduction of the median part of the basal sclerites. The flexors of the prelabium (*f*) have a more anterior origin.

In both nymph and adult the dorsal muscles of the salivarium (figs. 2C, 5D, 1*s*) have origin on the basal sclerites of the hypopharynx. In Orthopteroids these muscles have origin on the posterior part of the suspensorium of the hypopharynx.

(d) *The appendages.*

(i) *The antennae* (figs. 2B, 5E).—In both the nymph and the adult the pedicel (*pdc*) and flagellum are movable by extensor (6) and flexor (7) muscles having origin on the scape (*sc*). The extrinsic antennal muscles (4, 5) have origin on the dorsal arms of the tentorium (*dt*). The antenna thus shows the usual Pterygote condition. The antenna of Odonata is not described in the survey of antennal structure by Imms (1939).

(ii) *The mandibles* (figs. 2B, 6C, 7A).—These are similar in nymph and adult. They are toothed with incisor (*i*) and molar (*m*) regions. The mandibles show a primitive condition in that hypopharyngeal (*admdh*) and tentorial (*admdt*) adductors are present as well as the usual cranial abductors (8) and adductors (9). The mandibles, however, have anterior (*ama*) and posterior (*pma*) points of articulation.

(iii) *The maxillae* (figs. 3A, 7B).—These are similar in nymph and adult. Each maxilla lacks a galea. Of the two lobes present on the distal end of the stipes (*st*), the inner (*lc*) has been called a mala and the outer (*mplp*) a palp (Imms, 1951). Berlese (1901), Tillyard (1917), Lucas (1923) and Jeannel (1949) think that the inner lobe represents the lacinia and galea fused, and

that the outer lobe is a palp. Weber (1949) figures the inner toothed lobe as a lacinia and shows the stipital, although not the cranial, muscles of this part. This interpretation is probably correct. On the inner toothed lobe are inserted the characteristic cranial flexor of the lacinia (14) and stipital flexor of the lacinia (15). The outer lobe represents the maxillary palp (*mplp*). The maxillary palp of Orthopteroids has two characteristic muscles arising on the stipes. These muscles, the levator (17) and the depressor (18), are present in *Aeshna*, although the depressor is reduced. The evidence of the muscles is against this outer lobe being the galea, since the galea of the maxilla of Orthopteroids has but one muscle, a flexor, arising on the stipes.

Strenger (1952) has made a study of the musculature of the adult maxilla, and interprets the inner lobe as a lacinia and the outer as a galea. However, Strenger has noted only the levator muscle of the outer lobe and has missed the small depressor muscle The species examined by this author is *A. cyanea*, as in the present study.

(iv) *The labium.*—The labium, especially that of the nymph, is specialised, and has been the subject of much controversy (see Amans, 1881; Butler, 1904; Whedon, 1927; Táborský, 1927; Calvert, 1929; Munscheid, 1933; Snodgrass, 1954[1]).

In the nymph the labium (fig. 3B, C, D) consists of two regions separated by an articular line (*al*). These regions may be called the prelabium (*prlb*) and postlabium (*plb*). These names are given for convenience only, since the musculature does not support this interpretation. Corbet (1951, 1953) follows a similar procedure. The labial palps (*lplp*) are modified into prehensile hooks and the muscles of the palp, especially the depressor (29), are well developed. The depressors of the palp have origin on the supposed postlabium. In Orthopteroids these muscles have origin on the prelabium. The remaining muscles of the labium have no obvious homologues in Orthopteroids. A pair of extensor muscles (*e*) has origin on the tentorial bar (*tb*) and insertion on the postlabium and a pair of flexor muscles (*f*) has origin on the basal sclerites of the hypopharynx (*bsh*(*as*)) and insertion on the prelabium. A pair of accessory extensor muscles (*ae*) is situated in the postlabium and a pair of accessory flexor muscles (*af*) runs from the postlabium to the prelabium.

In the extension of the labium the contraction of the extensor muscle (*e*) swings the postlabium forward, the posterior surface of the proximal part of the postlabium pivoting on the basal sclerite of the hypopharynx. The contraction of the flexor muscle (*f*) will reverse this movement. Although the prelabium is pushed forward to some extent by the forward swing of the postlabium, the full extension of the prelabium cannot be explained by muscle contraction. Snodgrass (1954) gives evidence indicating that the protraction of the labium is caused by blood pressure. This appears to be the case for the prelabium at least, for, when the prelabium is extended, the membrane of the articular line between the pre- and postlabium can be seen to be distended with blood. The

[1] Snodgrass, R. E., 1954, The dragonfly larva. *Smithson. misc. Coll.* **123** (2): 38 pp., 11 figs. This paper was received while the present study was in press. In his section on the head Snodgrass concentrates mainly on the feeding apparatus. The present study essentially agrees with Snodgrass's account on all points.

accessory extensor muscles (*ae*) are small and do not appear to be important in the extension of the prelabium. The accessory flexors (*af*) have the function of folding the prelabium on the postlabium.

In the labium of the adult (fig. 7c) the levator of the palp and the extensor muscle are absent. Like Munscheid, I have been unable to see the extensor muscle described by Whedon. Munscheid has overlooked a pair of muscles (*rplb* (32)) inserting on the basal sclerite of the hypopharynx and having origin on the proximal part of the postlabium. (The word origin is used here to help a comparison of the places of attachment of this muscle in nymph and adult. It is not strictly correct since the postlabium is a movable part.) In the nymph these muscles run from the hypopharynx to the tentorial bar and are obviously homologous with the retractors of the hypopharynx of Orthopteroids. In metamorphosis these muscles shift their origin to the postlabium, where they function as retractors of the postlabium.

The reduction in the labial musculature of the adult is correlated with a reduction in mobility. The prehensile nature of the palps is reduced with a reduction in the muscles of the palp and the absence of the extensor muscles of the postlabium. The basal sclerites of the hypopharynx are also reduced.

The following is suggested as a reason for the shift in origin of the nymphal retractors of the hypopharynx. In retracting the postlabium of the adult at its posterior end this muscle will also tilt the labium as a whole posteriorly and act as an extensor. It is possible that, with a reduction in the prehensile function of the labium and the absence of the extensor muscle of the nymph, a substitute extensor has been formed by the shift in origin of the retractor of the hypopharynx. This substitute extensor inserting on the proximal end of the postlabium is capable of producing extension of the labium to a much smaller degree than the extensor muscle of the nymph inserting on the distal end of the postlabium.

5. List of Head Muscles.

1. Compressor of labrum.
2. Anterior retractor of labrum.
3. Posterior retractor of labrum.
4. Levator of antenna.
5. Depressor of antenna.
6. Extensor of flagellum.
7. Flexor of flagellum.
8. Abductor of mandible.
9. Adductor of mandible.
10. Promotor of cardo.
11. Adductor of cardo.
12. Proximal adductor of stipes.
13. *a*. Distal adductor of stipes arising on anterior arm of tentorium.

    b. Distal adductor of stipes arising on body of tentorium.
14. Cranial flexor of lacinia.
15. Stipital flexor of lacinia.
17. Levator of maxillary palp.
18. Depressor of maxillary palp.
28. Levator of labial palp.
29. Depressor of labial palp.
32. Retractor of hypopharynx of nymph.
33, 34. Anterior dilators of cibarium and buccal cavity.
35, 36, 39. Anterior dilators of pharynx or precerebral pharyngeal muscles.
37. Dorsal dilator of postpharynx.
38. Dorsal hypopharyngeal muscle.
41. Ventral dilator of buccal cavity.
42, 43. Ventral dilators of pharynx.
44. Ventral dilator of postpharynx.

6. Abbreviations Used on the Figures.

admdh, Hypopharyngeal adductor of mandible.
admdt, Tentorial adductor of mandible.
ae, Accessory extensor of labium.
af, Accessory flexor of labium.
e, Extensor of labium.
f, Flexor of labium.
rplb (32), Retractor of postlabium of adult. This muscle is homologous with the retractor of the hypopharynx of the nymph.
1*s*, Dorsal muscle of salivarium.
aclp, anteclypeus.
al, articular line.
ama, anterior mandibular articulation.
ant, antenna.
asc, antennal sclerite.
at, anterior tentorial arm.
bc, buccal cavity.
br, brain.
bsh, basal sclerite of hypopharynx in adult.
bsh(*as*), basal sclerite of hypopharynx or anchor sclerite in nymph.
cb, cibarium.
cd, cardo.
clp, clypeus.
decl, dorsal ecdysial cleavage line.
dt, dorsal arm of tentorium.
dtm, dorsal tentorial mark.
e, compound eye.
er, epistomal ridge.
es, epistomal sulcus.
fg, frontal ganglion.
for, foramen magnum.
fr, frons.
fra, frontal apodeme.
hs, hypostomal sulcus.
hyph, hypopharynx.
i, incisor region of mandible.
lb, labium.
lc, lacinia.
lig, ligula.
lm, labrum.
lplp, labial palp.
m, molar region of mandible.
md, mandible.
mh, movable hook of labium.
mplp, maxillary palp.
mx, maxilla.
mxa, point of articulation of maxilla.
o, ocellus.
oc, occipit.
ocs, occipital sulcus.
os, ocular sulcus.
or(*l*), left ocular ridge.
or(*r*), right ocular ridge.
p, pharynx.
pa, parietal region of cranium.
pclp, postclypeus.
pdc, pedicel of antenna.
pge, postgena.
plb, postlabium.
plst, pleurostoma.
pma, posterior mandibular articulation.
pmt, postmentum.
poc, postocciput.
pos, postoccipital sulcus.
pp, postpharynx.
pr, pleurostomal ridge.
prlb, prelabium.
prmt, prementum.
pt, posterior tentorial pit.
sc, scape of antenna.
sfra, sulcus of frontal apodeme.
sh, suspensorial sclerite of hypopharynx.
sld, salivary duct.
slr, salivary reservoir.
sog, suboesophageal ganglion.
st, stipes.
to, torma.
tb, tentorial bar.
vx, vertex.

7. Summary.

The morphology of the head of an Odonatan is described and compared with that of the head of Orthopteroids. The most significant features are :

The cranium is specialised with prominent strengthening ridges associated with the highly-developed compound eyes.

The tentorium is primitive in form and in the origin of the anterior arms from the pleurostomal part of the subgenal sulcus.

The basal sclerite of the hypopharynx of the nymph possesses a long, posterior, anchor-shaped projection. The postlabium pivots on this projection when the labium is extruded.

The mandibles possess the primitive hypopharyngeal and tentorial adductors as well as cranial muscles.

The maxillary musculature indicates that the maxillary galea is absent and that the two lobes on the distal end of the stipes are the lacinia and the maxillary palp.

The skeleton and musculature of the labium, especially the nymphal labium, are specialised. An explanation is offered of the functioning of the labium in nymph and adult. In metamorphosis the retractor of the hypopharynx of the nymph shifts its origin from the tentorium to the postlabium and functions as an extensor of the labium.

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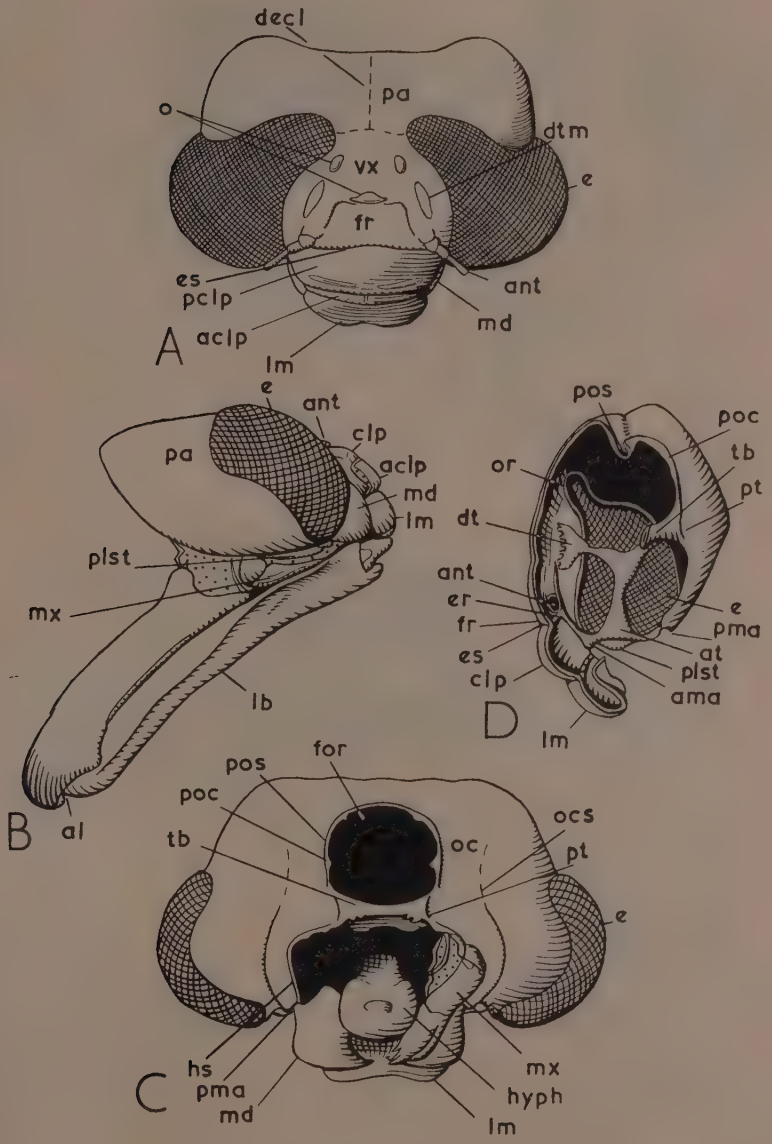

FIG. 1.—Head of nymph of *Aeshna cyanea* (Müller). A, Anterior view; B, lateral view; C, posterior view; D, lateral view of the cranium dissected to show the tentorium.

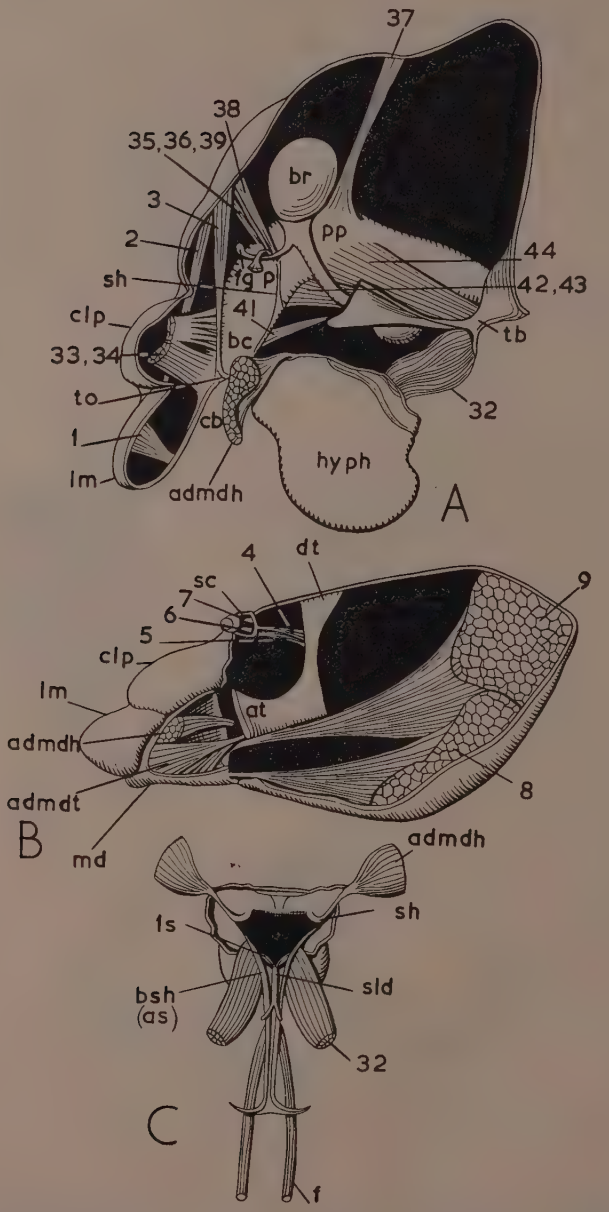

FIG. 2.—Head of nymph of *A. cyanea*. A, Lateral view of cranium dissected to show muscles of alimentary canal; B, lateral view of cranium dissected to show antennal and mandibular muscles; C, dorsal view of hypopharynx and associated muscles.

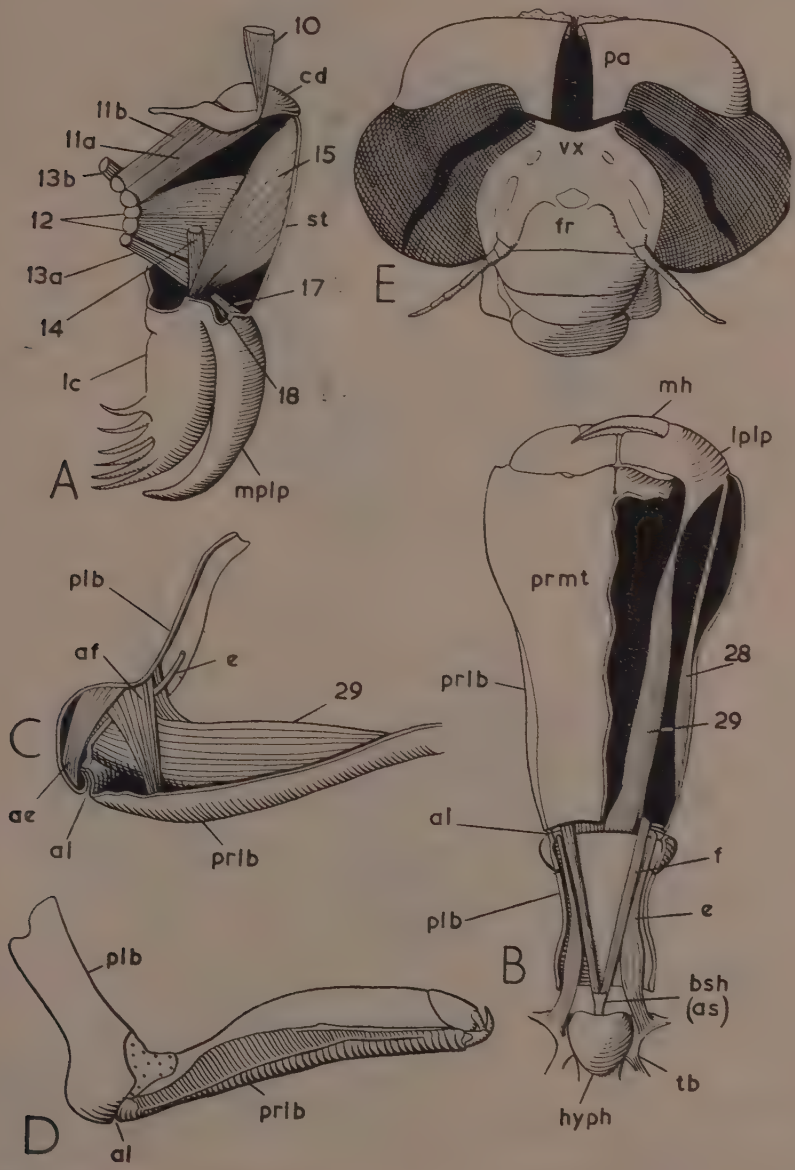

FIG. 3.—Head of nymph of *A. cyanea*. A, Lateral view of maxilla dissected to show muscles; B, dorsal view of extended labium dissected to show muscles; C, lateral view of part of labium dissected to show accessory muscles; D, lateral view of labium partly extended and showing distension of articular line membrane with blood; E, dorsal view of head exuviae of final instar nymph.

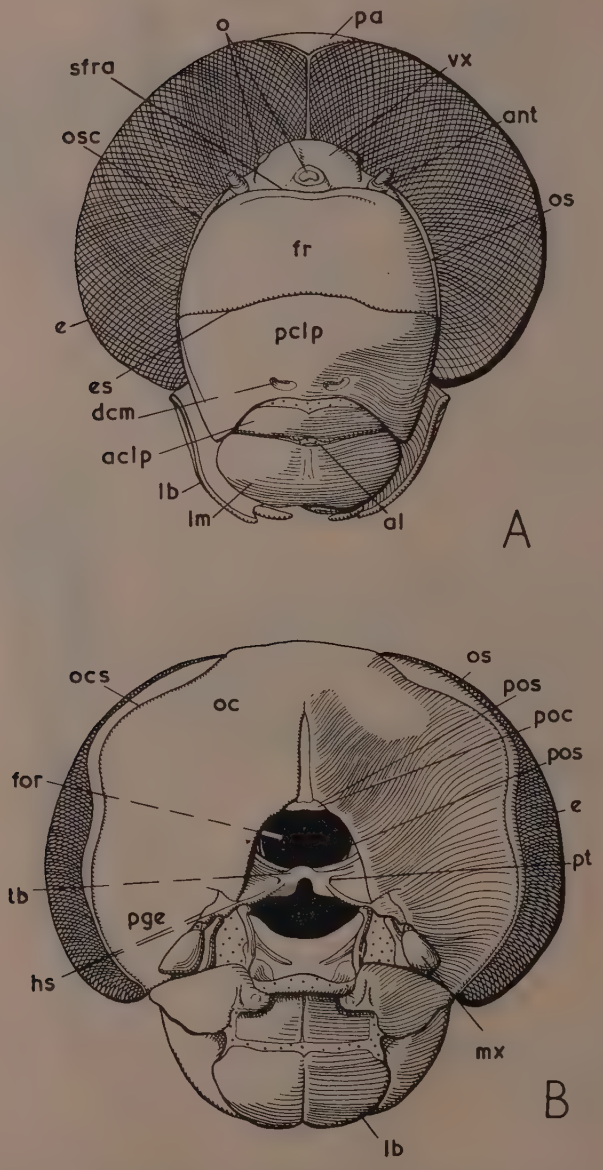

FIG. 4.—Head of adult of *A. cyanea*. A, Anterior view; B, posterior view.

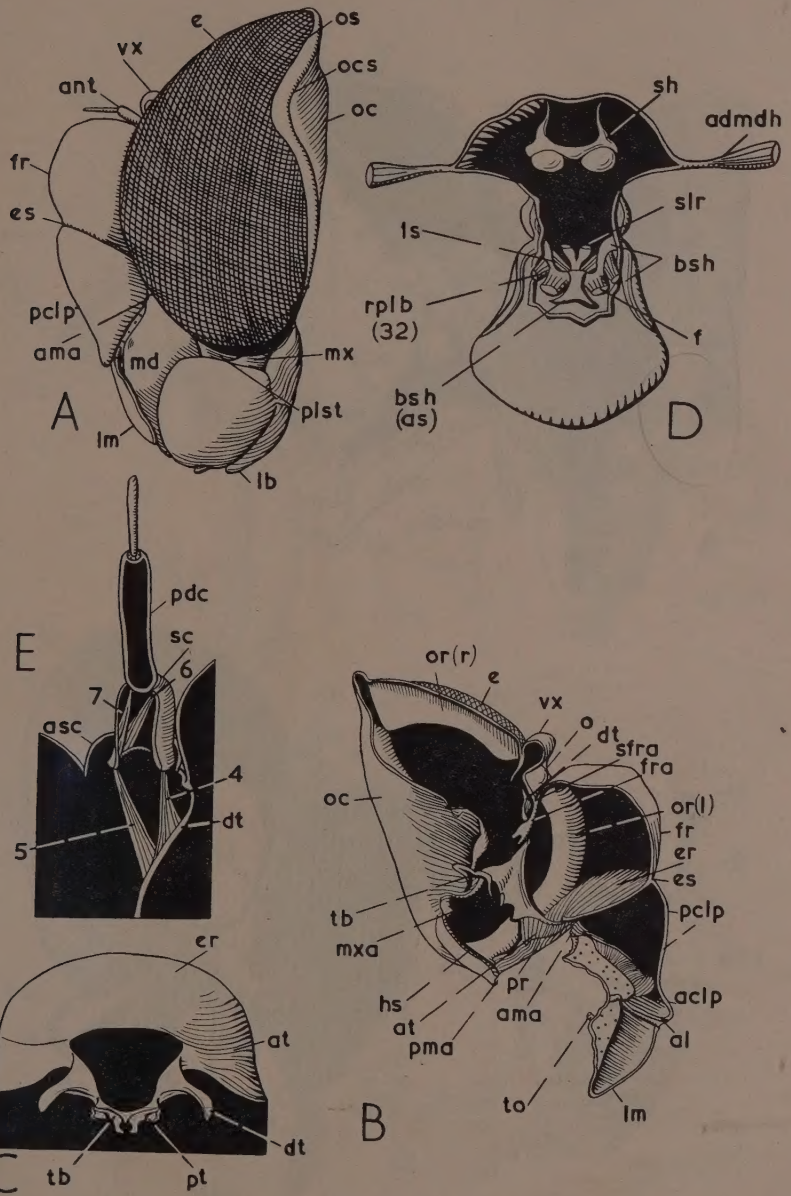

FIG. 5.—Head of adult of *A. cyanea*. A, Lateral view; B, lateral view dissected to show internal skeleton; C, dorsal view of tentorium; D, dorsal view of hypopharynx and associated muscles; E, lateral view of dissection of base of antenna and part of head to show antennal muscles.

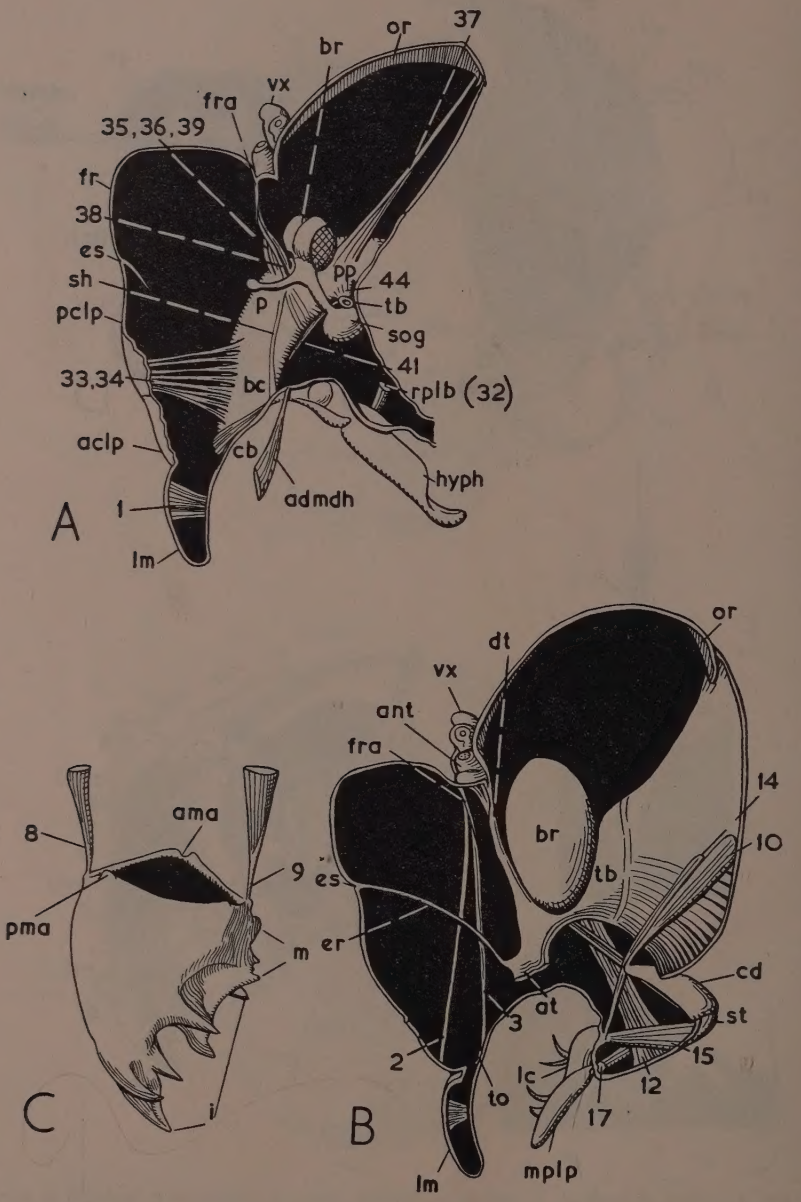

FIG. 6.—Head of adult of *A. cyanea*. A, Lateral view of cranium dissected to show muscles of alimentary canal; B, lateral view of head dissected to show labral and some maxillary muscles; C, posterior view of mandible.

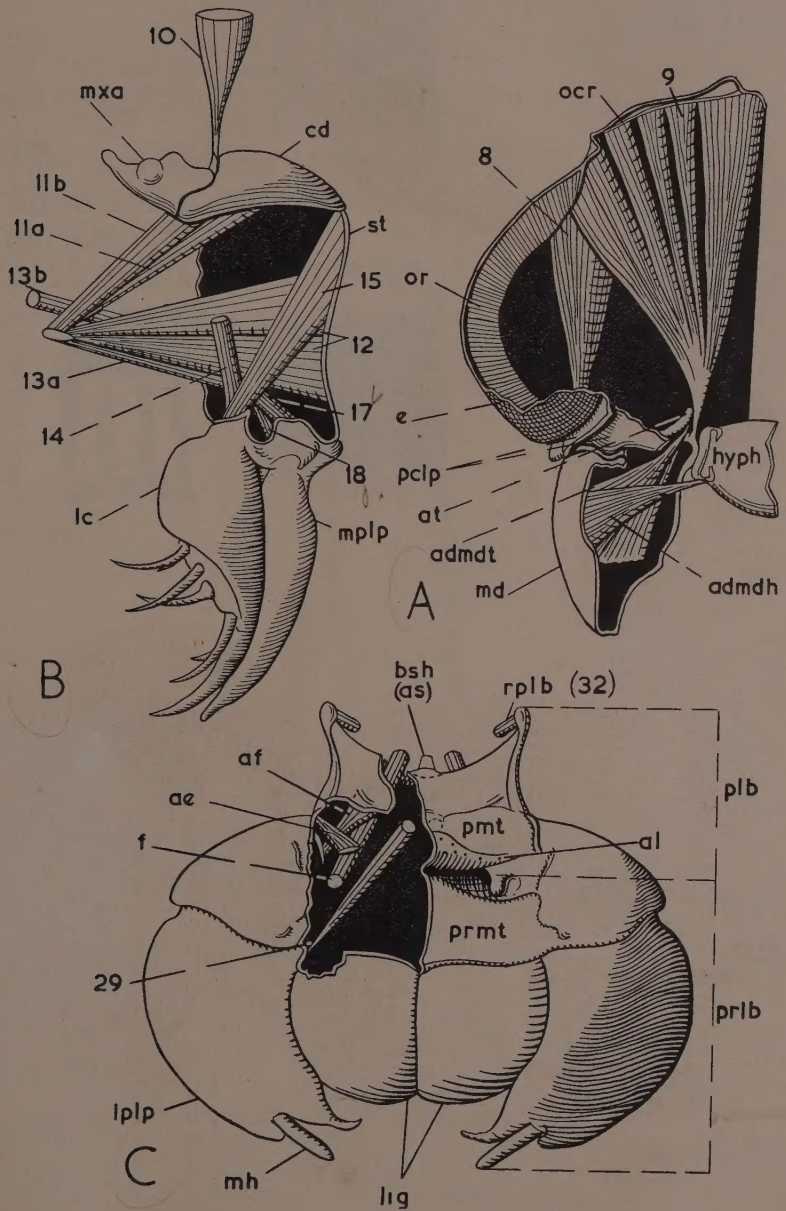

FIG. 7.—Head of adult of *A. cyanea*. A, Antero-lateral view of mandible and part of cranium dissected to show mandibular muscles; B, lateral view of maxilla dissected to show muscles; C, posterior view of labium dissected to show muscles.